

On the Inheritance of Coat Colour in Horses.

By C. C. HURST.

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Recent experiments by the writer have demonstrated the Mendelian inheritance of coat colour in rabbits.* These results suggested that the inheritance of coat colour in horses might also be in accordance with the Mendelian principles. In the case of horses, however, the ordinary method of direct experiment was impracticable, so that recourse was had to the valuable series of records contained in 'Weatherby's General Stud Book of Race Horses.' This work consists of 20 volumes, containing fairly complete records of the age, colour, sex, and parentage of British thoroughbreds from the earliest accounts down to the end of 1904.

In the modern volumes, at all events, these records have been carefully registered, and with the allowance of a small margin of error, may be safely accepted as scientific evidence, as the results of this paper show.

Professor Karl Pearson has already made use of this material in his paper "On the Inheritance of Coat Colour in Horses,"† but his statistical methods did not disclose any intrinsic differences in the heredity of the several colour-types. More recently, referring to the inheritance of eye and coat colour, Professor Pearson remarks that:—"Before we leave the cases above it is just worth reiterating that nothing corresponding to Mendel's principles appears in these characters for horses, dogs, and men."

In regard to thoroughbred horses, he adds:—"It is the same with every coat colour taken, its relative constancy depends largely on the extent to which it has appeared in the ancestry, and one by one black, bay, chestnut, grey must be dismissed by the Mendelian as neither 'recessive' nor 'dominant,' but as marking 'permanent and incorrigible mongrels.' "‡

A careful examination of the 'Stud Book' records so far fails to give any support to Professor Pearson's statement: on the contrary, the records show clearly, for instance, that bay and brown are Mendelian dominants to chestnut

* 'Journ. Linn. Soc. (Zool.),' vol. 29, pp. 283—324 (1905).

† 'Phil. Trans.,' A, vol. 195, pp. 79—150 (1900).

‡ 'Biometrika,' vol. 2, pp. 214, 215 (1903).

which is recessive.* For example, the bay and brown sires *St. Simon*, *St. Serf*, *Galopin*, *Ladas*, *Merry Hampton*, and *Cabin Boy*, mated with numerous chestnut mares, gave 370 foals, all of which were bays or browns. The following table gives the individual numbers :—

Table I (DD × RR).

Pure Dominant Bay and Brown Sires, Mated with Recessive Chestnut Mares.

Sires.	Bay and brown foals.	Chestnut foals.	Total.
<i>St. Simon</i>	96	0	96
<i>St. Serf</i>	83	0	83
<i>Galopin</i>	62	0	62
<i>Ladas</i>	56	0	56
<i>Merry Hampton</i>	44	0	44
<i>Cabin Boy</i>	29	0	29
Totals	370	0	370

The above numbers not only show the Mendelian dominance of bay and brown over chestnut, but they also prove that the individual sires concerned are homozygous bays and browns giving off no chestnut gametes.

It may be noted that all these sires had bay or brown parents and grandparents except *St. Serf*, which had a chestnut grandparent.

Further records show that other bay and brown sires are heterozygous, giving off chestnut gametes on the average in equal numbers, in accordance with the Mendelian expectation.

For instance, the bay and brown sires *Royal Hampton*, *Donovan*, *St. Angelo*, *Isinglass*, *Orvieto*, *Ayrshire*, *Florizel II*, *Pioneer*, *Isonomy*, *Melton*, *Wisdom*, and *Rose Window*, mated with numerous chestnut mares, gave 702 foals, of which 355 were bays and browns and 347 were chestnuts. These numbers are close to the Mendelian expectation of equality.

The following table gives the individual numbers :—

* In the recent volumes, about 95 per cent. of the colours registered are bay, brown, or chestnut, the small remainder consisting of black, grey, roan, and other colours.

Table II (DR × RR).

Impure Dominant Bay and Brown Sires, containing Chestnut, Mated with Recessive Chestnut Mares.

Sires.	Bay and brown foals.	Chestnut foals.	Total.
Royal Hampton	44	44	88
Donovan	47	33	80
St. Angelo.....	37	41	78
Isinglass	28	34	62
Orvieto	32	30	62
Ayrshire	31	29	60
Florizel II.....	34	25	59
Pioneer	26	26	52
Isonomy	25	24	49
Melton	20	23	43
Wisdom.....	18	23	41
Rose Window	13	15	28
Totals	355	347	702

Of the above heterozygous bay and brown sires containing chestnut, *Royal Hampton*, *St. Angelo*, *Isinglass*, *Orvieto*, *Isonomy*, *Melton*, and *Wisdom* had each a chestnut parent; *Donovan*, *Pioneer*, and *Rose Window* had both parents bay or brown, with a chestnut grandparent; *Ayrshire* had all the parents and grandparents bay or brown, with a chestnut great-grandparent; while *Florizel II* had all the parents, grandparents and great-grandparents bay or brown, with a chestnut great-great-grandparent. It will be noted that, notwithstanding these differences in ancestry, all are heterozygous, giving off chestnut gametes in about equal numbers, in accordance with the Mendelian expectation.

Further records show that the recessive chestnuts, variously extracted from bays and browns, as a rule breed true when mated together without reversion to their bay and brown ancestors, in accordance with the Mendelian conception of gametic purity.

For example, 100 chestnut sires, variously extracted, mated with about 600 chestnut mares of various extractions, gave 1104 foals, of which 1095 are recorded as chestnuts and 9 as bays or browns. That is to say, more than 99 per cent. of foals bred from chestnut parents are recorded as chestnuts, while less than 1 per cent. are recorded as exceptions to the rule. The apparent exceptions to the rule of chestnuts breeding true might have some significance if they were more numerous, but they are too inconsiderable to be of any certain value, and may simply represent breeders' or printers' errors.

In a work of such a magnitude and character as the 'General Stud Book,' it is satisfactory to find that in a given case, tested by Mendel's law, 1 per cent. covers the margin of error, and the result reflects great credit on all those concerned in the compilation of the records.

The following table gives the individual numbers of 30 of the chestnut sires:—

Table III (RR × RR).

Chestnut Sires, of Various Extractions, Mated with Chestnut Mares of Various Extractions.

Sires.	Bay and brown foals.	Chestnut foals.	Total.
Amphion	0	56	56
Kendal	1	49	50
Wiseman.....	1	48	49
Chittabob	0	45	45
Despair	0	45	45
Juggler	1	41	42
Otterburn	1	40	41
Bend Or	0	40	40
Ocean Wave	1	38	39
Deuce of Clubs	0	36	36
Orion	0	35	35
Sainfoin	0	28	28
Southampton	1	27	28
Esterling	0	27	27
Necromancer	0	27	27
Satiety	0	25	25
Saraband.....	0	24	24
Llanthony	1	23	24
Hagioscope.....	0	21	21
Timothy	0	19	19
Hazlehatch.....	0	18	18
Lowland Chief	0	18	18
Lord Lorne.....	0	17	17
Aperse	0	16	16
Albert Victor.....	0	16	16
Dan Dancer	0	16	16
Gold	0	15	15
Peter	0	13	13
Friar's Balsam	0	13	13
Young Woodpecker	0	11	11
Monte Cristo	0	11	11
Seventy other chestnut sires ..	2	237	239
Totals	9	1095	1104

It being established that chestnut is a Mendelian recessive, the question arises, What is the critical feature which distinguishes chestnut from bay and brown? An examination of many horses leaves little doubt that the chestnut is distinguished by the absence of black "points" (mane, tail, and legs) always present in bay and brown. In all these types the colour of the

coat presents a considerable range of tint. The differentiating pair of Mendelian characters is thus apparently the presence or absence of black pigment in the "points."

Summary.

In modern thoroughbred horses chestnut colour is a Mendelian recessive to bay and brown, which are dominant characters.

The consideration of other colours being excluded, bays and browns are of two kinds:—(a) Those that when mated with chestnuts will give *no* chestnut offspring. (b) Those that when mated with chestnuts will give, on an average, half their offspring chestnuts and the remainder bays or browns. Similarly, the recessive chestnuts, variously extracted from the dominant bays and browns, breed true, as a rule, when mated together, without reversion to their bay or brown ancestors. To this rule, 9 exceptions were found in 1104 cases, and it is not impossible that these may be due to errors in the records.

Note added January 31, 1906.

In the paper read on January 18, Professor Weldon disputes these conclusions, while admitting that, contrary to Professor Pearson's statement, chestnuts breed true within a very small percentage of error. Since my paper was read, a fresh tabulation has been made of a sample including more than 2500 offspring recorded from chestnut mares, taken without selection.

Omitting greys, two sires of doubtful identity and sires with less than 10 foals each, it appears that—

30 RR sires	give	455 R + 3D,
25 DD	„	450 D + 4R,
54 DR	„	496 D + 507 R.

This evidence, with that previously collected and with Professor Weldon's fresh evidence, points to about 1 per cent. of exceptions in the records of both the chestnuts and the pure dominants. Professor Weldon's argument is based entirely on the alleged existence of exceptions. The Stud Book is remarkably accurate, but there is a sufficient margin of demonstrable error in the returns to make it possible that the few exceptions which cannot be eliminated are due rather to mistake than to any physiological peculiarity in the animals concerned. As a matter of fact, a sensible proportion of the original records are afterwards corrected, either in the Stud Book itself or in the Racing Calendar. In illustration of this, it may be mentioned that

Ben Battle, a sire recorded in the Stud Book as chestnut, appears in the Racing Calendar several times as bay or brown, and Mr. G. H. Verrall, who has kindly given help in this matter, writes that it is practically certain that *Ben Battle* never ran as a chestnut.

Several alleged chestnuts, ascribed to *Hackler*, *Wolf's Crag*, and other pure dominant sires can be similarly corrected. Among the residual exceptions are some which were born dead or died unnamed. Very few indeed can be proved to have appeared in public uncorrected. Other errors probably arise through an incorrect return of the sire's name. For instance, a certain sire appears to give a total of 43 dominants and three chestnuts from chestnut mares; a scrutiny revealed that two of these chestnuts (which happen to be among the four mentioned above) were from one chestnut mare. Moreover, the same mare is credited with a *bay* foal by a *chestnut* sire. These three exceptions occur in four consecutive returns from one stud. Considering the extreme rarity of any exception, the coincidence seems to point to inaccuracy in the returns of the breeder in question. In Professor Weldon's tabulation such a sire would be ranked as a DR, and the 43 bays and browns he gave would go to create the excess of dominants which Professor Weldon found to result from the mating $RR \times DR$ —an excess obviously due to the inclusion of such cases in that category. It is, of course, not impossible that genuine exceptions do occur. They must, however, be exceedingly rare in any case, and I am disposed to doubt whether the returns made to the Stud Book have the extreme precision which would be required to establish such occurrences.

Finally, it would appear that the distinct properties of chestnuts must be ascribed to segregation rather than to ancestry, seeing that their behaviour in heredity is entirely different from that of bays and browns,¹ though their ancestral composition may for several generations have been the same.

This analysis was undertaken without any knowledge of previous work on similar lines, but several papers stating more or less concordant conclusions have since been discovered. The memoir by Crampe,* mentioned by Professor Weldon in the discussion on his paper of January 18, gives, as I now find, extensive tables drawn from German sources, showing that within a small margin of error chestnut (*fuchs*) breeds true. Of the exceptions, several, as he shows, are probably mistakes, and the rest he regards as dubious. Wilckens,† as the result of a similar analysis on a large scale, found 24 recorded exceptions to the purity of "*fuchs*" per 1000 matings. The absolute purity of chestnuts, however bred, is asserted by Mr. Wilfrid

* Landw., J. B., 1888, vol. 17, especially p. 828.

† *Ibid.*, p. 575.

Scawen Blunt* for the Kehailan strain of Arabs. The same assertion is also made for the horses called "*rote*" (? red chestnut) in the Jutland breed by Jensen.† Finally, we have a general statement by Hayes,‡ applicable to all kinds of horses, that in the vast majority of cases a foal from a chestnut dam by a chestnut sire is of a chestnut colour.

The existence of the two kinds of dominants, and the conclusions based thereon have not, so far as I know, been previously recognised.

Note on the Offspring of Thoroughbred Chestnut Mares.

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The colours of English thoroughbred race-horses, as recorded in Weatherby's General Stud-Book, are grouped under the six main categories—Grey, Roan, Chestnut, Bay, Brown, Black; but each category includes a considerable range of colour, and intermediates occur with quite sensible frequency. At the meeting of the Royal Society, held on December 7 last, the suggestion was made that the relation between the most important colours, Chestnut, Bay, and Brown, might be expressed by a simple Mendelian formula—Bay or Brown being regarded as determined by one Mendelian unit, which was "dominant" to the "recessive" Chestnut. In discussing this suggestion, I made certain statements, which I promised to justify as soon as possible, by offering the data, on which they were based, for publication. The object of the present note is partly to fulfil my promise, and partly to call attention to certain facts which must be considered in the attempt to apply any Mendelian formula whatever to the inheritance of coat colour in race-horses.

I have taken from Weatherby's Stud-Book a fairly complete record of all the foals produced in England by Chestnut mares during the period (rather more than eight years) covered by vols. 18 and 19. All cases of doubtful paternity have been excluded, and I have not tried to obtain external evidence in the few cases where the colour of sire or of foal is omitted. With

* 'The Nineteenth Century and After,' 1906, January, p. 63.

† 'Deut. Pferdezucht,' I, Hft. 11, 1904. (Original not seen; abstract in 'J. B. Landw. Pfl. u. Tierzüchtung,' 1905, II, p. 273.)

‡ 'Points of the Horse' (3rd ed.), 1904, p. 326.